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GENETIC VARIATION AND POPULATION STRUCTURE OF THE ENDANGERED SNAIL KITE IN SOUTH FLORIDA

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ABSTRACT.—Ten enzymatic stains were used to resolve the products of 12 loci for 150 snail kite (*Rostrhamus sociabilis*) nestlings from four major wetlands in south Florida. Nine loci were monomorphic across all sites; two loci were only slightly polymorphic, with overall allele frequencies <0.05. Average expected heterozygosity among all individuals was 4.6% (range = 0–25%). Average heterozygosity across the four sites ranged from 4.1–5.2%. Mean percent polymorphic loci (0.99 level) was 18.2% (range = 8.3–25%). Overall F_{ST} was 3.4%, which was significantly different from 0; F_{IS} and F_{IT} values suggested a slight heterozygote deficiency. The largest genetic distance was consistently between Lake Okeechobee and the other sites; the shortest genetic distances were between Lake Kissimmee and Conservation Area 2B and between Conservation Area 2B and Conservation Area 3A. Gene flow was estimated at 7.1 migrants per generation. Short genetic distances among the four wetlands in south Florida suggest little differentiation among these populations of snail kites.

KEY WORDS: *snail kite*; Rostrhamus sociabilis; *Florida*; *electrophoresis*; *population genetics*.

Variación genética y estructura poblacional de *Rostrhamus sociabilis* en peligro, en el sur de Florida

RESUMEN.—Diez colorantes enzimáticos fueron usados para analizar los productos de 12 loci para 150 polluelos de la especie *Rostrhamus sociabilis*, de los cuatro mayores humedales en el sur de Florida. Nueve loci fueron monomórficos a través de todos los sitios; dos loci fueron ligeramente polimórficos, con una frecuencia alélica total <0.05. El promedio esperado de heterozigocidad entre todos los individuos fue 4.6% (rango = 0–25%). El promedio de heterozigocidad a través de los cuatro sitios tuvo rangos entre 4.1–5.2%. La media porcentual de loci polimórficos (nivel 0.99) fue 18.2% (rango = 8.3–25%). F_{ST} total fue 3.4%, significativamente diferente de 0; los valores de F_{IS} y F_{IT} sugieren un suave deficiencia heterozigotica. Consistentemente, la mayor distancia genética fue entre el Lago Okeechobee y los demás sitios; las menores distancias genéticas se registraron entre el Lago Kissimmee y el Area de Conservación 2B y entre el Area de Conservación 2B y el Area de Conservación 3A. El flujo genético fue estimado en 7.1 migrantes por generación. Las pequeñas distancias genéticas entre los cuatro humedales del sur de Florida sugieren poca diferenciación entre las poblaciones de *R. sociabilis*.

[Traducción de Ivan Lazo]

The snail kite (*Rostrhamus sociabilis*) occurs widely in tropical Central and South America, Cuba and Florida (Sykes et al. 1995). *R. s. plumbeus* is restricted to Cuba and southern Florida. Movement between Florida and Cuba is doubtful given

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the lack of foraging habitat in extreme south Florida (e.g., Florida Bay and Keys), the short-distance nomadic dispersal shown in Florida and the relatively large expanse of open water separating Florida and Cuba. The original breeding range in Florida primarily consisted of the headwaters of the St. Johns River northward to the Oklawaha drainage, the Kissimmee River basin (including Lake Kissimmee), southward through Lake Okeechobee, the Everglades and freshwater marshes near Florida Bay (Sykes 1984). However, by the late 1960s Sykes (1984) found kites mostly at Lake Okeechobee, Conservation Area 1 (Loxahatchee NWR), Conservation Area 2A, Conservation Area 2B (CA2B) and the southern portion of Conservation Area 3A (CA3A). These conservation areas are large impounded remnants of the Everglades habitat that once extended from Lake Okeechobee to the northern edge of Everglades National Park. The range of snail kites became further reduced to the marshes on the west side of Lake Okeechobee and the southern region of CA2B and CA3A during the 1970s (Sykes 1984). The range decline in Florida along with the large-scale decrease in numbers of kites resulted in the species being listed as endangered on the initial federal endangered species list in 1967 (Fed. Reg. 42[155]:40685–40688). It was similarly listed as endangered on the initial state of Florida list in 1972.

Considerable inter-year variation has occurred in the numbers of snail kites found at individual wetlands in Florida during the 1970s and 1980s (Beissinger and Takekawa 1983, Rodgers et al. 1988, Takekawa and Beissinger 1989, Bennetts et al. 1994). These fluctuations often were associated with low water levels and droughts that force the birds to disperse to other wetlands. Based on nest monitoring and sightings of color-banded birds, kites dispersed from the southern parts of their range and recolonized their former nesting range at Lake Kissimmee, Lake Tohopekaliga, East Lake Tohopekaliga, the upper St. Johns River marshes in Indian River County and several smaller wetlands in Hendry and Okeechobee counties during a particularly severe drought in the late 1980s (Sykes et al. 1995). Apparently, lack of suitable foraging habitat and decreased availability of apple snails (*Pomacea paludosa*), precludes recolonization farther north.

Because of these recent fluctuations both in the size and range of this relict population within Florida, the snail kite warrants a genetics study to determine if it has experienced loss of genetic variability due to population bottlenecks. The objectives of our study were therefore to (1) document the level of genetic variability in populations nesting in four major wetlands in south Florida and (2) estimate levels of genetic differentiation among these populations. This information would provide insight into the effects of dispersal on population genetics and allow management decisions to be made regarding snail kite recovery in the state of Florida.

METHODS

Our study was conducted under the Florida Administrative Code, General Purpose Wildlife Code 39-9.002, subsection 2, that permits Florida Game and Fresh Water Fish Commission personnel and cooperating investigators to handle birds for specific purposes of approved research. Feather tissues also were collected under the authority of the Endangered Species Cooperative Agreement between the U.S. Fish and Wildlife Service and the Florida Game and Fresh Water Fish Commission. Our field work followed the American Ornithologists' Union guidelines for scientists conducting research on wild birds (Oring et al. 1988).

We collected tissue samples from snail kite nestlings in the four major wetlands (Lake Kissimmee, Lake Okeechobee, CA2B, CA3A) of the species' range in south Florida during 1987 (Fig. 1). One growing, centrally-located secondary feather from each wing was removed from one nestling (3–4 wk of age) per nest. Feathers were frozen in liquid nitrogen within 1 min after removal and subsequently stored in an ultra-cold freezer (−76°C) until electrophoresed. Laboratory (Stangel 1986) and field (Stangel and Lennartz 1988) studies indicate that feather removal is not detrimental to survival or growth of even small birds.

Pulp was squeezed from the feather shafts and homogenized with 5 ml of 0.01 M Tris-0.001 M EDTA pH 7.0 buffer solution. Electrophoretic conditions and general staining procedures followed those techniques of Selander et al. (1971), Harris and Hopkinson (1976) and Barman (1985). Loci were numbered according to the mobility of their products from anode to cathode. Allozymes were designated alphabetically in order of relative mobility from anode to cathode, with the letter "C" chosen to represent the most common allele.

The statistical package BIOSYS-1 (Swofford and Selander 1981) was used for analysis of snail kite allelic frequencies, genetic variability measures (Hardy-Weinberg expected heterozygosity, mean number of alleles per locus, percent polymorphic loci), deviations from expected Hardy-Weinberg proportions, Nei's (1978) and Rogers' (1972) genetic distances and F-statistics (Nei 1977, Wright 1978). Gene flow, or Nm (N = deme size and m = migration rate among demes), was calculated using Wright's (1943) formula: $F_{ST} = 1/(4Nm + 1)$.

Patterns of population structure can be revealed through analysis of allele frequencies using Wright's F-statistics (Wright 1978). The most commonly used statistic, F_{ST}, is a measure of the extent that a species shows spatial

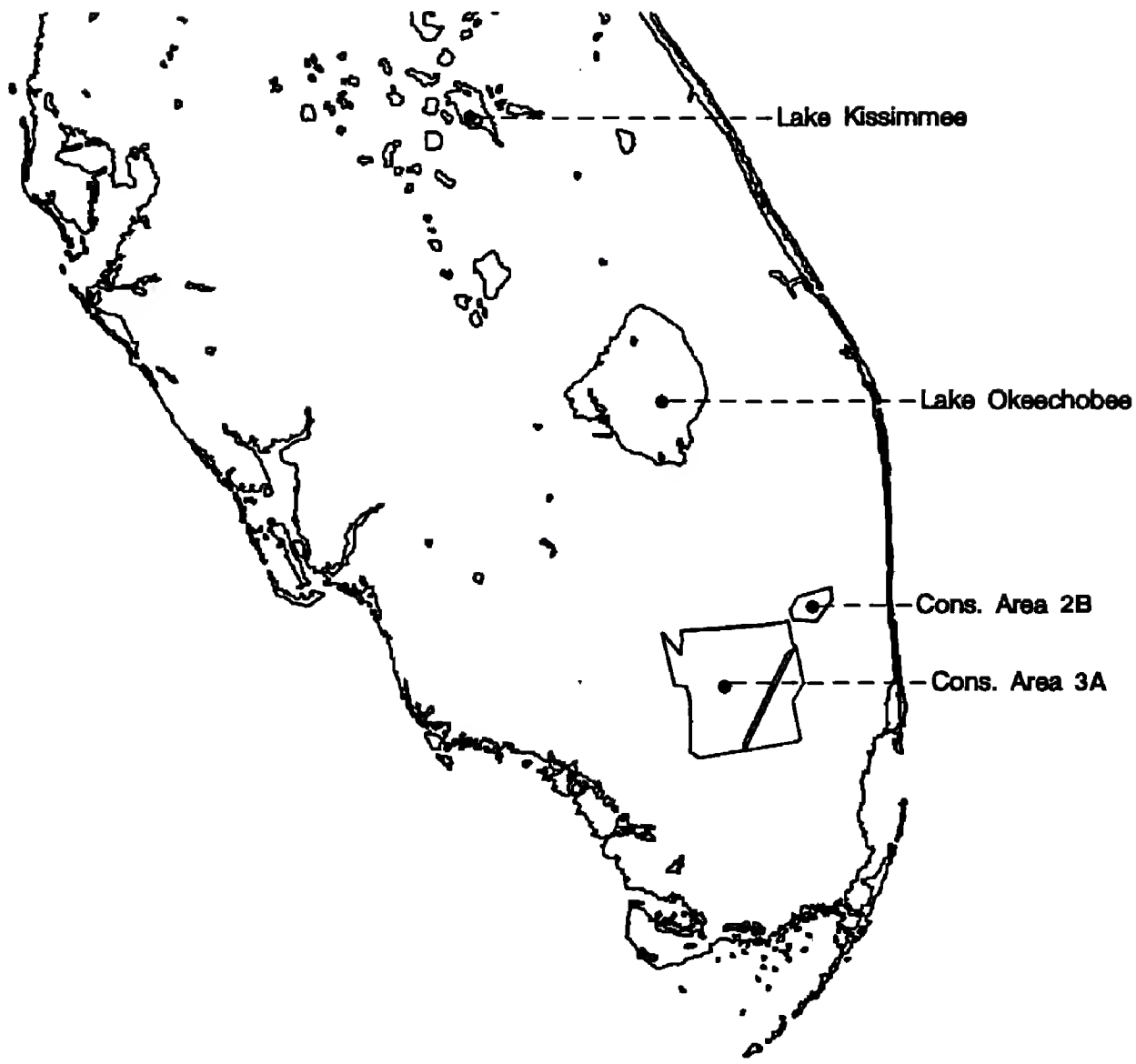

Figure 1. Sources of tissue samples from snail kite nestlings at four wetlands in south Florida.

genetic heterogeneity. F_{ST} values range from 0, suggesting lack of differentiation or panmixia, to 1, indicating fixation of alternative alleles and complete differentiation. F_{IS} and F_{IT} are measures of heterozygote deficiency or excess within subpopulations (e.g., the four wetlands in our study) and the total population, respectively, and are commonly used as inbreeding indices. Both values range from -1 to 1, with positive values indicating heterozygote deficiency, which may occur with inbreeding. Precise interpretation of F-statistics requires detailed knowledge about the breeding structure of the species examined. Because this information is lacking in the snail kite, inferences about population structure cannot be made unambiguously.

RESULTS

Ten enzymatic stains were used to resolve the products of 12 loci for 150 snail kite nestlings from the four wetland sites. All individuals were scored for all loci. Nine loci were monomorphic across all sites; two loci were only slightly polymorphic (Pgd and Tri) and a single locus (Pep) exhibited three alleles, with overall allele frequencies <0.05 (Appendix 1). There was no convincing evidence for significant deviation from Hardy-Weinberg proportions.

Average expected heterozygosity among all individuals was 4.6% and ranged from 0–25%; the most heterozygous individual was therefore variable at 3 of 12 loci. Fifty-two percent of all individuals were monomorphic, 43% were heterozygous at one locus, 4% were heterozygous at two loci and one individual was heterozygous at three loci. Average heterozygosity across the four sites ranged from 4.1–5.2% (Table 1). Percent polymorphic loci (0.99 level) ranged from 8.3–25%, with a species mean of 18.2%. Mean number of alleles per locus ranged from 1.1–1.3, with a mean of 1.2.

Table 1. Genetic variability at 12 loci for snail kites from four wetlands in south Florida. Standard errors are in parentheses.

SITE	*N*	MEAN NUMBER OF ALLELES PER LOCUS	PERCENTAGE OF LOCI POLYMORPHIC (0.99)	MEAN HETEROZYGOSITY HARDY-WEINBERG EXPECTED (×100)
Kissimmee	24	1.1 (0.1)	8.3	4.2 (4.2)
Okeechobee	24	1.3 (0.1)	25.0	5.2 (3.7)
Cons. Area 2B	26	1.2 (0.1)	16.7	4.2 (3.8)
Cons. Area 3A	76	1.1 (0.1)	8.3	4.1 (4.1)

Table 2. F-statistics for three polymorphic loci in snail kites from south Florida.

LOCUS	F_{IS}	F_{IT}	F_{ST}
Phosophogluconate dehydrogenase (Pgd)	0.064	0.096	0.035
Peptidase phynylproline (Pep)	−0.046	−0.015	0.030
Tripeptide aminopeptidase (Tri)	−0.041	−0.010	0.030
Mean	0.053	0.085	0.034

The frequency of the common allele ("C") at the Pgd locus ranged from 0.438–0.667 (Appendix 1), which was significantly different from 0 among sites ($\chi^2_3 = 8.4$, $P = 0.037$). Three private polymorphisms (alleles detected at only one site) were identified: Pep "D" allele at CA3A; Pep "B" allele at CA2B; and Tri "D" allele at CA3A.

An overall F_{ST} of 3.4% was significantly different from 0 ($\chi^2_{16} = 37.5$, $P < 0.005$; Table 2). F_{IS} and F_{IT} values were on average positive, suggesting a slight heterozygote deficiency. Mean Nei's genetic distance among sites was 0.002 (range = 0.000–0.004). Mean Rogers' genetic distance among sites was 0.014 (range = 0.006–0.027). The largest genetic distances using both methods were consistently between Lake Okeechobee and the other sites (Nei's distance: 0.002–0.004; Rogers' distance: 0.014–0.027), whereas, the shortest genetic distances were between Lake Kissimmee and CA2B (Nei's distance: 0.000; Rogers' distance: 0.006) and between CA2B and CA3A (Nei's distance: 0.000; Rogers' distance: 0.008). Gene flow, or the estimated number of migrants per generation, was 7.1.

DISCUSSION

Heterozygosity in the snail kite (4.6%) was slightly lower than the average of 6.5% (range = 0–30.7%) for 86 species of birds reported by Evans (1987). However, average percent polymorphic loci (18.2) and alleles per locus (1.2) of kites were within the range of those reported for other bird species (Barrowclough et al. 1985, Evans 1987). Because we lack data for comparisons with populations outside of Florida and historical populations of snail kites in the state, we do not know if the current level of heterozygosity in Florida is similar for the species over its entire range, or differs because of founder effects when the species originally colonized Florida and/or population bottlenecks experienced during population decreases that occurred in the 1960s.

Reported population fluctuations in the snail kite (Beissinger and Takekawa 1983, Rodgers et al. 1988, Takekawa and Beissinger 1989, Bennetts et al. 1994) might have affected heterozygosity, although population bottlenecks would have to be severe and last several generations to have a significant effect (Nei et al. 1975). The presence of three private polymorphisms suggests that these conditions have not occurred and the historical reduction in the south Florida population does not seem to have affected levels of genetic variation. Heterozygosity in the snail kite varied from 4.1% to 5.2% at the population level, which is within typical values for birds (Evans 1987).

Genetic differentiation among snail kites in the four wetlands we sampled was low, as it is for most species of birds (Evans 1987). An F_{ST} of 0.034 in the snail kite suggests that only about 3.4% of the total genetic variation detected can be accounted for by heterogeneity among sites, with the remaining 96.6% accounted for within sites. Evans (1987) reported an average of 4.8% of the variation occurs among populations for 23 avian species he examined. Short genetic distances among the four wetlands in south Florida also suggest little differentiation among these populations of snail kites.

Although habitat fragmentation tends to contribute to smaller, more isolated populations, the ability of birds to fly would be expected to increase gene flow and contribute to lack of genetic differentiation among even distant sites. Periodic population shifts by snail kites from the Everglades conservation areas caused by changing hydrologic con-

ditions likely increases gene flow among the south Florida wetlands used as breeding sites. Periodic low water levels that cause kites to disperse can result in low recruitment, increased adult mortality and population decreases (Beissinger 1995). Kites also exhibit extensive annual movements that seem to have nothing to do with hydrologic conditions (Bennetts and Kitchens 1992, 1993). The estimated 7.1 migrants per generation calculated from F_{ST} using Wright's (1943) formula further suggests high levels of interchange among south Florida demes. Ideally, the exchange of animals should be pulsed and occur at times when inbreeding has become great enough such that outbreeding will yield optimum levels of heterosis (Chesser et al. 1980). Thus, even with the snail kite population subdivided among south Florida wetlands, the stochastic nature of drought events should contribute to pulsed exchange of individuals that would be able to maintain heterozygosity and a vigorous population.

That the snail kites at Lake Okeechobee were slightly more genetically distant than kites at the other three wetlands is interesting, but the genetic distances are very short and must be interpreted cautiously. Kites were rarely observed and did not breed at Lake Kissimmee during the 1960s and 1970s (Sykes 1984). Kites began to breed at Lake Kissimmee during the early 1980s when drought conditions forced them to abandon the Everglades (e.g., CA2B and CA3A). The reason why kites from the Everglades would pass Lake Okeechobee and move farther north to Lake Kissimmee is unclear. Perhaps a drawdown of the lake in 1979 for fisheries management restored suitable foraging conditions that facilitated the recolonizing of Lake Kissimmee. However, until more is known about the response of apple snails to another drawdown of the lake during 1996, we are reluctant to speculate further. Recolonization also may have been due to the large number of kites that already occupied Lake Okeechobee and concurrent low lake levels during the early 1980s. Perhaps the breeding subpopulation at Lake Okeechobee is more stable than those at the other three major wetlands. Whereas lake levels, amount of flooded marsh and number of kites vary among years (Rodgers 1992), some littoral zone at Lake Okeechobee always is available for foraging and nesting. If the other wetlands flood and dry out as the result of frequent, extreme hydrological changes, there may be considerable exchange of kites among these sites that increases their genetic similarity relative to Lake Okeechobee. Zink et al. (1987) also found more similarity between farthest separated populations of California Quail (*Callipepla californica*) than nearest geographic neighbors.

The logical next step for genetic studies of the snail kite would be to sample populations in Cuba and South and Central America where the species is common and widespread (Beissinger 1983, Beissinger et al. 1983). Comparisons with the south Florida population would provide insight into genetic differentiation and hence, gene flow between these sites. It also would be interesting to compare these areas to see if the south Florida population exhibits reduced genetic variability relative to the larger and potentially more stable and representative South American populations.

CONSERVATION IMPLICATIONS

The results of this study provide benchmark snail kite genetic variability measures against which values obtained in the future can be compared. If future population fluctuations reduce snail kite numbers to very low levels, it would then be possible to determine if genetic variability had been reduced relative to our values.

Translocation of individuals from larger populations is one strategy to increase small populations but consideration must be given to the genetic characteristics of both donor and recipient populations to lessen the chance of disrupting locally adapted populations (Avise and Nelson 1989, Stangel et al. 1992). Although translocation of kites has not been considered to date, our data can serve as a reference for managers considering translocation of genetically similar snail kites to south Florida if ever conditions warrant such a drastic recovery strategy.

With the exception of the Lake Okeechobee subpopulation, we found few distinctions among the snail kite demes in south Florida. The Lake Okeechobee subpopulation should receive further study, particularly with regard to the movement of successfully breeding kites into and out of this wetland relative to other wetlands. Kites have exhibited a tendency to concentrate their population in CA3A during some years (Sykes 1984, Rodgers et al. 1988, Bennetts et al. 1994, Sykes et al. 1995). A large number of an endangered species at a single site is a poor conservation strategy from a genetic point of view. However, extensive annual movements by kites often result in considerable inter-

change of birds among wetlands in south Florida (Bennetts and Kitchens 1992, 1993). The challenge will be to maintain a continued interchange of individuals among these sites for a high degree of genetic polymorphism while at the same time minimizing the effects of inbreeding within each wetland in south Florida.

The population and distribution fluctuations of snail kites in south Florida are so dramatic that demographic concerns probably outweigh immediate genetic threats and these should receive greatest attention in conservation plans. Appropriate demographic and habitat management of the snail kite will prevent the loss of genetic variability due to population bottlenecks.

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Appendix 1. Allele frequencies and electrophoretic conditions for three polymorphic loci of snail kites from four wetlands in south Florida.[a]

Enzyme Locus Allele	Enzyme Commission Number[b]	Wetland			
		Kissimmee	Okeechobee	Cons. Area 2B	Cons. Area 3A
Phosphogluconic dehydrogenase (Pgd)	1.1.1.43				
C		0.604	0.438	0.654	0.667
D		0.396	0.563	0.346	0.333
Phenylalanyl-proline peptidase (Pep)	3.4.13.9				
B		0.000	0.000	0.019	0.000
C		1.000	1.000	0.981	0.947
D		0.000	0.000	0.000	0.053
Tripeptide aminopeptidase[c] (Tri)	3.4.1.4				
C		1.000	1.000	1.000	0.961
D		0.000	0.000	0.000	0.039

[a] The following 9 loci were monomorphic in all individuals assayed: malic dehydrogenase-1 and malic dehydrogenase-2 (1.1.1.37); lactate dehydrogenase-1 (1.1.1.27); phosphogluco-isomerase (5.3.1.8); creatinine kinase-1 and creatinine kinase-2 (2.7.3.2); isocitrate dehydrogenase-1 (1.1.1.42); phosphoglucomutase (5.4.2.2); leucine aminopeptidase (3.4.11).

[b] Enzyme commission number from Barman (1985).

[c] Substrate for tripeptide aminopeptidase was leucylglycylglycine.